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Spatio-temporal dynamics of *Codium* populations along the rocky shores of N and NW Spain

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ABSTRACT

The green alga *Codium fragile* ssp. *fragile* (hereafter *C. fragile*) has long been assumed to outcompete and displace its native congeners via cryptic invasion. We analysed the population dynamics of the exotic *C. fragile* and native congeners and their relative abundance on intertidal shores in N-NW Spain. Our results did not support the existence of current competitive displacement by the exotic species. The presence of *C. fragile* was clearly seasonal, while the native *C. tomentosum* was more persistent throughout the year, due to a higher frequency of frond sprouting from perennial basal fragments. However, our results also indicated an increase in the proportion of *C. fragile* relative to native species towards inner areas of the Bay of Biscay, which was correlated with environmental gradients. The greater tolerance of *C. fragile* to environmental stress and its opportunistic abilities may favour establishment and spread of the species under a warming scenario.

1. Introduction

The introduction and establishment of non-indigenous species (NIS) is considered one of the greatest threats to the integrity of most ecosystems on earth (Simberloff et al., 2014; Davidson et al., 2015) and continues to be one the most commonly studied processes (Davidson et al., 2015). Although only a small proportion of introduced NIS become invasive (Blackburn et al., 2011), these species may have measurable effects on the recipient habitats. The impacts include displacement of native species, biodiversity loss, changes in community structure and food webs, and alterations in ecosystem processes (Molnar et al., 2008; Simberloff et al., 2014).

Climate change is expected to alter spatial and temporal patterns of species distribution and resource availability, thus enhancing biological invasions (Occhipinti-Ambrogi, 2007). For instance, NIS that are capable of tolerating a wider range of thermal regimes may be more successful under a scenario of increasing temperature (Hellmann et al., 2008; Walther et al., 2009). Human activities such as maritime transport and aquaculture have also contributed to increased numbers and impacts of NIS on marine systems in recent decades (e.g. Cohen and Carlton, 1998; Occhipinti-Ambrogi, 2007).

Seaweeds are an important component of marine invasions worldwide, with around 300 species detected in coastal systems (Trowbridge, 1998, 2006; Johnson and Chapman, 2007; Williams and Smith, 2007). Recent meta-analyses indicate strong negative impacts of invasive seaweeds on resident assemblages, particularly at the same trophic level through competitive interactions, although the number of species analysed was small relative to the total number detected (Thomsen et al., 2009; Maggi et al., 2015). Moreover, the number of NIS may still be underestimated, mainly due to cryptic invasions, i.e. in cases where NIS are morphologically similar to native species (Carlton and Scanlon, 1985; Mackie et al., 2012). Detection of cryptic invasions is crucial for quantifying both the numbers of invaders and their impacts on ecosystems. Several incidences of cryptic invasions involving both algae and invertebrate groups have been reported in marine environments (Thomsen et al., 2006; Lee, 2016).

The siphonous green macroalga *Codium fragile* ssp. *fragile* (Suringar) Hariot (Provan et al., 2008) (hereafter *C. fragile*) is a typical example of a cryptic invasive species. Originating in Japan, *C. fragile* is now widely distributed across the world (Trowbridge, 1996; Campbell, 1999; Provan et al., 2008; Guiry and Guiry, 2017). Although considered a warm-temperate alga (Fralick and Mathieson, 1972; Carlton and Scanlon, 1985), its distribution spans from across temperate and cold regions of the NW and NE Atlantic (Trowbridge, 1998; Matheson et al., 2014). The potential impacts of the introduction of *C. fragile* have been widely studied, and both negative and positive effects have been identified (Bulleri et al., 2006; Scheibling and Gagnon, 2006; Drouin et al., 2016). *C. fragile* has long been assumed to outcompete and

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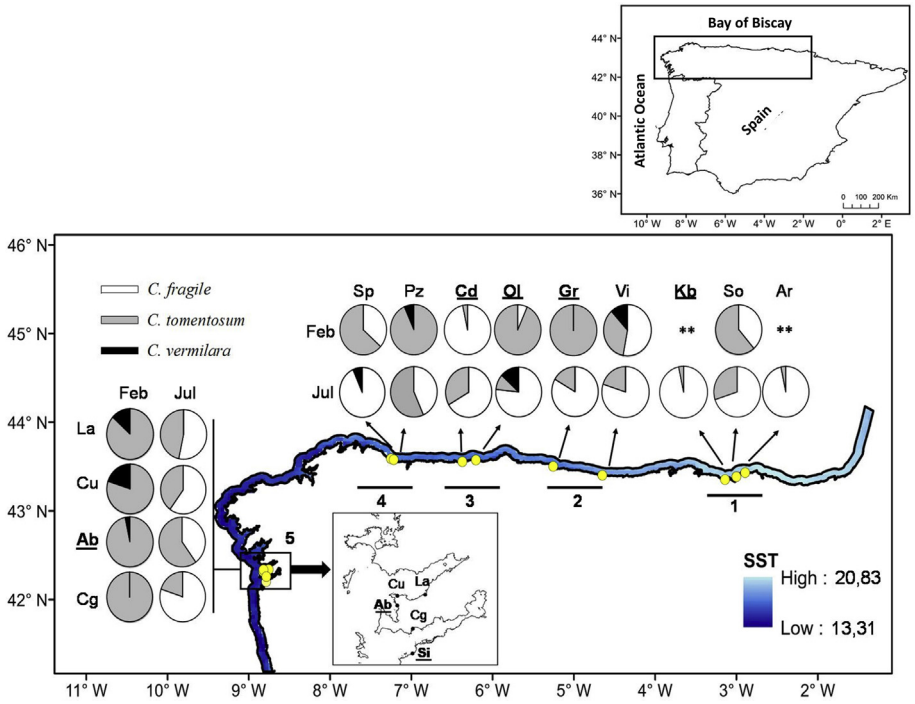

Fig. 1. Frequency of occurrence of *Codium* species in each stretch of coast and location studied, and SST satellite data (annual average values from the period 2013–2016). *Codium* occurrence, n = 30 for all locations, except Vidiago (Vi) in February (n = 11). Coastal stretches are represented by numbers and underlined with a dashed line (1 = Basque Country, 2 = E Asturias, 3 = W Asturias, 4 = N Galicia, 5 = western Atlantic shores). Ar: Armintza; So: Sopela; Kb: Kobaron; Vi: Vidiago; Gr: La Griega; Ol: Oleiros; Cd: Cadavedo; Pz: Peizás; Sp: San Pedro; La: Lapamán; Cu: Cabo Udra; Ab: Área de Bon; Cg: Cangas; Si: Sirenita. The name of those locations where the temporal dynamics of *Codium* spp. were determined are shown in bold type and underlined. ** indicates locations that were visited but no *Codium* fronds were found.

ultimately displace its native congeners (Trowbridge, 2001 and references therein). However, elucidating, rather than assuming, the dynamics of the relationships between congeners (i.e. displacement *vs* coexistence) demands quantitative information about population growth and the phenology of *Codium* species in the different regions where *C. fragile* has been introduced (e.g. Trowbridge, 2001; Trowbridge and Farnham, 2004; Trowbridge and Farnham, 2009; Geraldi et al., 2014).

The success of *C. fragile* has been linked to its various modes of reproduction (Trowbridge, 1998; Bégin and Scheibling, 2003) and to its greater tolerance to high seawater temperature, irradiance and desiccation stress than in the native congeners (Burrows, 1991; Yang et al., 1997; Trowbridge, 1998). As this species may be nitrogen-limited during most of the growing season, its growth and spread may also be favoured increased concentrations of nutrients in seawater (e.g. eutrophication, upwelling events) (Trowbridge, 1998). In this context, the presence of utricle hairs may be important for enhancing nitrogen assimilation in this species (Oates and Cole, 1994; Harrison and Hurd, 2001).

The establishment and regional spread of NIS depends on propagule pressure (Williamson, 1996), biotic resistance and life history traits of the invader (Sakai et al., 2001; Lockwood et al., 2005), as well as on the presence of suitable environmental conditions (Sakai et al., 2001). In N-NW Spain, there are regional differences in abiotic factors, such as seawater temperature and inorganic nutrient content (Ramos et al., 2012), mainly as a result of upwelling phenomena that occur during spring-summer, generally towards western areas (Botas et al., 1990; Álvarez et al., 2010). In this region, *C. fragile* coexists on intertidal rocky shores with three erect native *Codium* species: *C. tomentosum* Stackhouse, *C. vermilara* (Olivi) Chiaje, and *C. decorticatum* (Woodward) Howe (Fernández-Montero et al., 1998; Bárbara et al., 2005; Rodríguez and Moliner, 2010; Rojo et al., 2014). Invasive and native species are all dichotomously branched and morphologically very similar. The subspecies *C. fragile* ssp. *atlanticum* (Cotton) Silva is now considered a native of the British Isles (Provan et al., 2008) and has been also cited in N Spain. However, no specimens have been identified by molecular analysis in the area (Rojo et al., 2014).

The results of some preliminary studies in the region indicated that, relative to its native congeners, *C. fragile* occurs more frequently towards the inner part of the Bay of Biscay, either on emergent substrata or in tide pools (Cires Rodríguez and Rico Ordás, 2007; Rojo et al., 2014). This suggests that increases in SST, already observed in N-NW Spain (Gómez-Gesteira et al., 2008; Costoya et al., 2015), may lead to changes in abundance, survival and persistence of *C. fragile*, as also suggested Armitage and Sjøtun (2017) in a study conducted on Norwegian shores.

The present study constitutes an extended analysis of the relative abundance and population dynamics of native and exotic *Codium* species along N-NW coasts of Spain. We focused on the phenology and growth patterns of invasive and native congeners, which are very variable in invaded regions and essential for understanding the invasive process and for enabling realistic predictions to be made about ecological impacts (Trowbridge, 1998). We also discussed the potential impact of the exotic species in a region in which a sharp environmental gradient is predicted under future climate change scenarios. The present study is one of few to quantitatively evaluate population dynamics of *Codium* species on intertidal shores (Trowbridge, 1996; Campbell, 1999; Bégin and Scheibling, 2003; Schmidt and Scheibling, 2005).

2. Material and methods

2.1. Study sites

The study was conducted at low intertidal levels in 14 locations in 5 selected stretches of coasts in N − NW Spain. The distribution of the coastal stretches ranged from the inner part of the Bay of Biscay to western Atlantic shores (in the outer part of rias or coastal inlets). Specifically, four stretches were located on the northern coasts, in the Bay of Biscay (Basque Country, E Asturias, W Asturias and Lugo), and another was located in the western Atlantic coast (stretches numbered 1 to 5 in Fig. 1). Between 2 and 5 sampling locations, all gently sloping rocky platforms semi-exposed to wave action, were chosen within the coastal stretches. Well-developed *Bifurcaria bifurcata* R. Ross beds dominate at low intertidal levels in these locations, and this perennial seaweed is abundant all along the N and NW coasts of Spain, co-dominating with *Himanthalia elongata* on Atlantic shores (Niell, 1977; Fernández et al., 1983). *Codium* species appeared at low intertidal levels and in tide pools (when present) in these locations. The tidal

regime is semidiurnal in the region, with a maximum tidal range of about 4.2 m in the Bay of Biscay, and 4 m in Atlantic locations (Carballo et al., 2009).

2.2. Environmental variables

Seawater temperature and inorganic nutrients were measured at 6 locations, i.e. those where the analysis of temporal dynamics of *Codium* spp. was carried out (see below): Kobaron, La Griega, Oleiros, Cadavedo (Bay of Biscay), and Área de Bon and Sirenita (western Atlantic; see Fig. 1). Seawater temperature was measured with Tidbit loggers (Onset Corporation, MA, USA) fixed with screws to the rocky substratum at roughly 1.0 m above the Lowest Astronomical Tide (LAT) in each location. This tidal level corresponded to the middle of the *B. bifurcata* zone and is profusely colonized by *Codium* species in the 6 study locations. The loggers recorded temperature every 30 min between April 2015 to September 2016. Data were periodically downloaded and only one single reading per tidal cycle, the reading closest to the high tide (54–60 monthly readings), was used to characterize the temporal and spatial variation in sea surface temperature (SST). Additionally, SST data of the N-NW coast of Spain were obtained from images taken by the Advanced Very High-Resolution Radiometer (AVHRR) available in the Jet Propulsion Laboratory Physical Oceanography Distributed Active Archive Center (JPL PODAAC). Annual average SST values for the period 2013–2016 were taken from monthly estimates at a spatial resolution of 4 km^2.

Triplicate water samples were obtained for analysis of dissolved nitrate, nitrite, and phosphate in the same 6 locations, at roughly 2-month intervals between July 2015 and July 2016. Seawater was filtered with polycarbonate filters (0.2 μm pore size) and stored frozen in 25 ml plastic tubes until analysis in a Skalar auto-analyzer (Skalar, SAN + +).

2.3. Field monitoring

The proportions of native and invasive *Codium* species were estimated in the 14 locations on the selected coastal stretches (Fig. 1). At each location, a linear transect of approximately 200–300 m was established parallel to the coastline, in the middle of the *Bifurcaria* zone (roughly between 1.0 and 0.7 m above Lowest Astronomical Tide, LAT). Samples were collected during low spring tides in February and July 2016. Branch tips from 30 thalli were randomly collected along the line transect (only 11 fronds were found at Vidiago in February). At four locations where tide pools were present (Peizás, Lapamán, Cabo Udra and Área de Bon), 30 additional thalli of *Codium* spp. were collected at random from these habitats. The species were identified in the laboratory by microscopy. The presence/absence of mucronate utricles, the size (diameter) of utricles and the position of the utricle hairs or hair scars in the absence of mucronate utricles were the main features used to identify the species (Silva, 1955; Burrows, 1991; Brodie et al., 2007). The presence or absence of gametangia and utricle hairs each specimen was also noted.

In addition, in 6 of the 14 locations, i.e. the most profusely colonized by *Codium* spp., were selected for study the temporal population dynamics of the species; four of the locations were in the Bay of Biscay and two were on western Atlantic shores (Fig. 1). Kobaron, in the Basque Country, was subsequently omitted from this temporal survey, as all the *Codium* fronds (all of them identified as *C. fragile*) disappeared from the sampling plots six months after the start of the study.

Six permanent plots (50 × 50 cm) were selected in each location in May 2015 (July 2015, in the case of La Griega). Plots were located in the middle of the *B. bifurcata* zone, where *Codium* species are common. The upper two corners of the plots were marked with screws and coloured plastic tags. The position of each individual (i.e. typically formed by several erect dichotomously branched thalli arising from a common spongy basal disc) was determined by measuring the distance to the two screws. For each specimen, we measured the maximum length, from the base of the holdfast to the tip of the longest frond, and the maximum circumference (maximum circumference of the bunch of fronds). Short, wide specimens forming continuous mats were occasionally observed in the plots. In these cases, the width was estimated as the surface area occupied. The percentage cover of *Codium* spp. was estimated per plot and date by summing the surface area occupied by each specimen (circle areas were estimated from maximum circumferences). All new erect thalli "recruits" (usually < 5 cm length) were also recorded for each site/date. Moreover, tips of length 2–3 cm were collected from 2 to 4 branches of each specimen for subsequent microscopic identification of the species in the laboratory. The branch tips of the same specimen (i.e. branches arising from a common basal disc) were not identified as different species in any of the cases. Samples were frozen at −18 °C until further analysis. Sampling of permanent plots was carried out at roughly 2 months intervals between May 2015 and September 2016.

2.4. Data analysis

The Pearson correlation coefficient was calculated with the proportion of *C. fragile* in the studied locations and the annual SST (average values from 2013 to 2016, satellite data). Differences in the counts of native (*C. tomentosum* + *C. vermilara*, see results) and invasive *Codium* species were analysed across coastal stretches (zones) by using a Generalized Linear Model for count data and categorical variables, with Poisson distributions of error terms and a log link function (i.e. log-linear models for analyses of contingency tables, Crawley, 2007). The analysis was carried out with data from July, when both native/invasive *Codium* spp. were present in the samples. The full saturated model included two factors and their interaction: Species Status (native *vs* invasive) and Zone (five zones: Basque Country, E Asturias, W Asturias, N Galicia and western Atlantic shores).

Differences in the counts of native and invasive *Codium* species between habitats (emerged substrata *vs* tide pools) were also evaluated using a log-linear model with three factors: Species Status (native *vs* invasive), Habitat (*Bifurcaria* zone vs tide pools) and Location (4 locations: Área de Bon, Cabo Udra, Lapaman and Peizás). In this case, only data from July in those locations where both habitats were sampled were considered.

Log-linear models were also used to test differences between *C. tomentosum* (the most abundant native species, see results) and the invasive *C. fragile* in relation to the proportion of individuals with gametangia and utricle hairs. In the first case, the analysis was only conducted with data from February (as individuals bearing gametangia were only detected in this month, see results), and for those locations with a relatively high abundance of both native and invasive species (San Pedro, Vidiago and Sopela, see results). Three factors were thus considered in the analysis: species (*C. tomentosum vs C. fragile*), reproductive status (presence or absence of gametangia) and location (3 locations). For the log-linear model of the proportion of individuals with utricle hairs, the following factors were included: Species (*C. tomentosum vs C. fragile*), Hairs (presence *vs* absence) and Location (9 locations). In this case, the analysis was carried out with data from July, when utricle hairs were well developed and only for the Bay of Biscay locations, where both native/invasive species were recorded.

In all those log-linear models, model selection followed a hypothesis testing approach. The saturated model with zero residual deviance (with as many parameters as number of data of the response variable) was first fitted and then simplified by removing the highest order interaction terms, with analysis of deviance conducted at each step (Crawley, 2007).

A two-way analysis of variance with Year and Locality as orthogonal and random factors was used to test for temporal and spatial differences in the maximum mean length of thalli of the native *C. tomentosum*. The data from September (the month with maximum average value for most of the locations and species, see results) were included in the analysis.

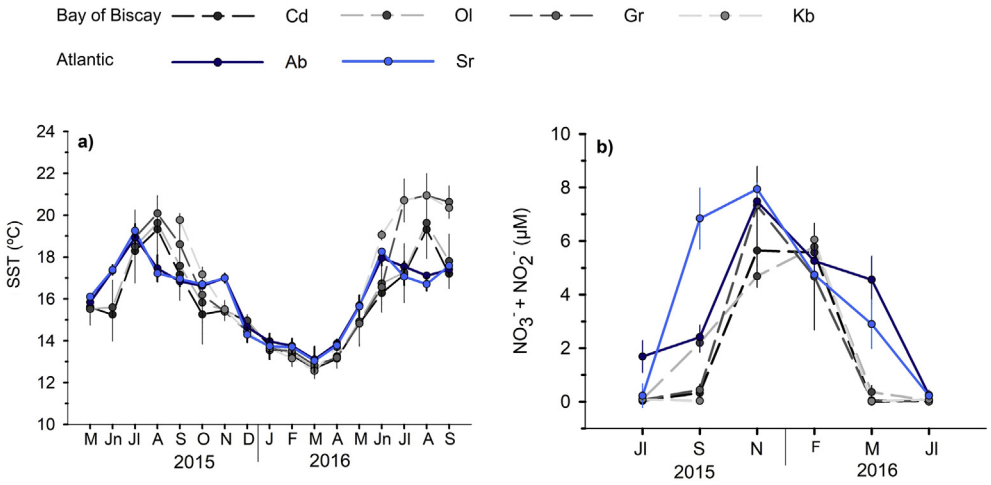

Fig. 2. Environmental factors a) monthly seawater temperature for field monitoring locations (± SE, n = 54–60), b) nitrite + nitrate concentration in seawater (± SE, n = 3), two-month intervals between July 2015 and July 2016.

Data were balanced (n = 37, i.e. the minimum number of fronds sampled per location). Homogeneity of variance was first examined using Cochran's test (Quinn and Keough, 2002) and data were log-transformed to fit this assumption. When the tests indicated significant differences, post hoc analysis was conducted using the Student – Newman – Keuls multiple comparison test (Quinn and Keough, 2002).

All statistical analyses were performed with R 3.0.3 software (R Development Core Team, 2011).

3. Results

3.1. Environmental variables

The average seawater temperatures were higher during summer months in locations on the northern coast (Bay of Biscay), especially in those locations towards the inner areas, La Griega and Kobaron (Gri, Kb, see Fig. 2a), than in those of western Atlantic shores. There was a time lag in the peak of temperature between those areas, as maximum average values were recorded in June–July on Atlantic shores and in August in the Bay of Biscay (Fig. 2a). Satellite data clearly show the gradient in mean SST, increasing from the Atlantic to the inner part of the Bay of Biscay (Fig. 1). The temperature data obtained *in situ* and those from satellite imagery were strongly correlated (Pearson's $r = 0.89$, $n = 6$, $p < 0.05$, for average SST data of July 2016).

Inorganic nutrient availability also differed between coastal areas. The nitrite and nitrate concentrations and nutrient availability were higher in the Atlantic locations than in the Bay of Biscay (e.g. compare September and May average values between locations, Fig. 2b). Similarly, average phosphate concentrations were higher throughout the year in Atlantic locations than in the Bay of Biscay (see Supplementary Material, S.M.1).

3.2. Relative abundance of codium species in NW Spain

The relative proportions of native and invasive species varied across dates and locations (Fig. 1). Two native erect species were found in transects: *Codium vermilara* (only found in some localities at low frequency) and the more abundant *C. tomentosum*. No specimens of *C. decorticatum* were observed in this study. The invasive species *C. fragile* was overall more abundant in July than in February 2016, except in Cadavedo (Fig. 1). In July, a higher proportion of invasive *C. fragile* appeared towards the inner part of the Bay of Biscay, and increased gradually from the western Atlantic coast to the Basque Country (Fig. 1, *C. fragile* proportions from coastal stretches, numbers 5 to 1 = 58.3, 68.3, 71.7, 81.7 and 87.8% respectively; Table 1a, significant interaction Zone x Species Status). This gradual increase was related to the pattern of average seawater temperature, increasing from western Atlantic shores towards the inner part of the Bay of Biscay (Fig. 3; marginally significant correlation between annual SST -average values from 2013 to 2016, satellite data- and proportion of *C. fragile*, Pearson's $r = 0.78$, $p = 0.05$, $n = 13$). In those locations where both transects and permanent plots were established, the proportions of native and

Table 1
Analysis of Deviance for log-linear models to test the effects of a) Zone (Zn, five zones, see Fig. 1), b) Habitat (Hab, *Bifurcaria* zone *vs* Tidepools) and Location (Loc, 4 localities, see methods) on the proportion of invasive and native *Codium* spp. (Sp, Species Status). The saturated model (M1) and nested models without interactions (M2, M3, M4) were compared to test for the presence of significant three-way or two way-interactions.

Model		Deviance	df	Δ Dev.	Δ df	p
a)	M1, Saturated and Final	0.000	0			
	M2, (-Zn x Sp)	19.94	4	−19.94	−4	< 0.001
b)	M1, Saturated	0.000	0			
	M2, (-Hab x Loc x Sp)	3.803	3	−3.803	−3	0.284
	M3, (-Hab x Loc x Sp, -Loc x Sp)	10.787	6	−6.984	−3	0.072
	M4 (-Hab x Loc x Sp, -Hab x Sp)	3.957	4	−0.155	−1	0.694

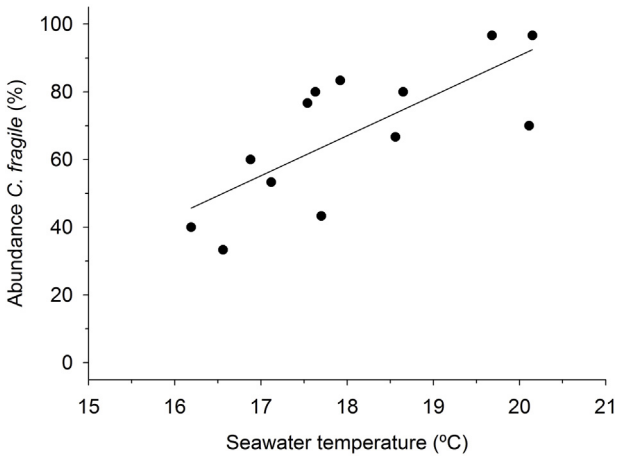

Fig. 3. Scatter plot of the relationship between SST (annual average value for the period 2013–2016, satellite data) and the percentage cover of *Codium fragile* in the surveyed localities.

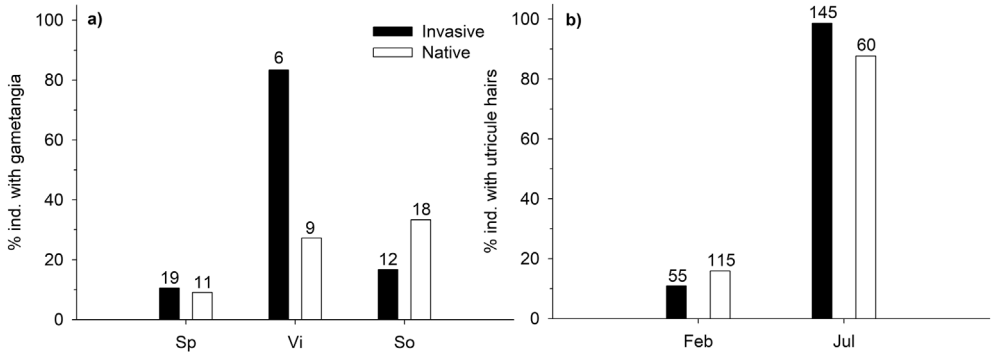

Fig. 4. Percentage number of individuals a) bearing gametangia and b) with utricle hairs in native *C. tomentosum* and invasive *C. fragile.* In a) data from February; Abbreviations for the locations, as in Fig. 1.

invasive species were calculated by including both types of records. As with the data derived from transects only, the predominance of the invasive species in July *vs* February, and the gradual increase in *C. fragile* from western Atlantic shores to the inner areas of the Bay of Biscay were still evident (see Supplementary Material, S.M.2 for details).

No significant differences in the proportion of native *vs* invasive species were detected between habitats (percentage of *C. fragile* in *B. bifurcata* zone = 49.46%; in tide pools = 46.66%, n = 120 in both cases; non-significant interaction Habitat x Species Status, Table 1b).

For both *C. tomensotum* and *C. fragile*, individuals bearing gametangia were mainly observed in February; in July only 1 individual of *C. fragile* (from a total of 108 sampled specimens) presented gametangia, while no specimens of *C. tomentosum* were reproductive (over a total of 282). In February, differences between the proportions of *C. tomentosum* and *C. fragile* individuals with gametangia was spatially variable (i.e. tended to differ between localities, Fig. 4a; interaction Locality x Species x Reproductive Status, p = 0.09, Table 2a). The proportion of reproductive specimens was highest for *C. fragile* in Vidiago, although the sample size was small (n = 6). On the other hand, the presence of utricle hairs was much more frequent in July than in February (Fig. 4b). In July, utricle hairs were more frequent in individuals of the invasive *C. fragile* than in the native *C. tomentosum* (significant interaction Species x Hair, Table 2b).

3.3. Growth rate and recruitment

Only the dynamics of the native species *C. tomentosum* and the invasive *C. fragile* were recorded, as the presence of *C. vermilara* was very scarce in the permanent plots and was only found in two of the studied locations. *C. tomentosum* was the only species appearing on western Atlantic shores (Sirenita and Área de Bon) in the plots (Fig. 5a and b and 6). Both *C. tomentosum* and *C. fragile* were recorded at the other locations in the Bay of Biscay (Cadavedo, Oleiros, La Griega), still with a clear dominance in terms of cover and number of individuals for the native species (Fig. 5c–f and 6). Finally, *C. fragile* was the only species present at Kobaron, the easternmost location in the Bay of Biscay, although all the fronds disappeared from the sampling plots six months after the start of the study (and therefore, this location was subsequently omitted from the temporal survey, see material and methods).

The length and percentage cover of both the native and the invasive species were maximal during summer, i.e. either July or September in most locations (Fig. 5). *C. tomentosum* reached larger sizes (maximum lengths) in locations on the western Atlantic shores, especially in Área de Bon, than in the Bay of Biscay (Fig. 5a,c). These patterns were variable between years (Table 3, significant interaction Location x Year). The lengths of *C. tomentosum* and the invasive *C. fragile* were almost identical in the northern coast locations in the Bay of Biscay (Cd, Ol, Gr; Fig. 5c,e). However, in those northern locations, the percentage cover of the native *C. tomentosum* was greater than that of the invasive species (Fig. 5d,f). The maximum values, with nearly 100% cover, were recorded for the native species in July at two locations in the Bay of Biscay, although in different years (Fig. 5d).

In accordance with the patterns of percentage cover, the number of individuals in permanent plots was much larger for *C. tomentosum* than *C. fragile* (Bay of Biscay locations: Cd, Ol, Gr in Fig. 6). The presence of *C. fragile* in the plots was minimal in February. Recruitment was greater for both species during spring-summer (May–September) with the lowest values observed in November and February, except in Área de Bon, where recruits appeared throughout the year (Ab, Fig. 6). In one location (La Griega, Gr), recruitment in July 2015 could not be estimated, because the sampling only began in July at the site (see material and methods). The thallus lifespan was short for both the native and invasive species, as only a small proportion of the recruits recorded in July 2015 remained more than one year in the plots, i.e. until July 2016. One-year old individuals were significantly less abundant in the invasive than the native populations: 1 of 18 thalli of *C. fragile* persisted until July 2016 (data pooled across localities of Bay of Biscay, Cd, Ol, Gr) and 5 of 15 thalli of *C. tomentosum* (Chi-squared = 4.244 df = 1, p = 0.039). These enduring individuals remained in February as perennating basal discs sprouting as erect thalli again in May 2016. Some of the new fronds (recruits) appearing in May 2016 were sprouts arising from remnant basal fragments. The percentage of sprouts varied depending on the location and species, ranging from 9.8% up to 64.7% in the case of *C. tomentosum* (from Oleiros to Cadavedo, n = 41 and 17 respectively) and from 0 to 33% in *C. fragile* (n = 25 to 9). Occasionally, continuous mats of *C. tomentosum* produced independent thalli, and the fusion of separate thalli into one large *Codium* mat was also observed the next growing season (7.17% and 3.17% for mats division

Table 2
Analysis of Deviance for log-linear models to test a) the effect of Species (Sp, *C. tomentosum vs C. fragile*) and Location (Loc) on the proportion of individuals bearing gametangia (Repro) and b) the effect of Species and Locality in the proportion of individuals with utricle hairs (Hair). a) included data from February and 3 locations (see material and methods). b) included data from July and the 9 locations on the northern coast (Bay of Biscay). In the analyses, the saturated model (M1) and models without interactions (M2, M3, M4) were compared to check for the presence of significant three-way or two way-interactions.

Model		Deviance	df	Δ Dev.	Δ df	p
a)	M1, Saturated and Final	0.000	0			
	M2, (-Loc x Sp x Repro)	4.779	2	−4.779	−2	0.092
b)	M1, Saturated Final	0.000	0			
	M2, (-Loc x Sp x Hair)	4.140	8	−4.140	−8	0.844
	M3, (-Loc x Sp x Hair, -Loc x Sp)	29.279	16	−25.139	−8	< 0.001
	M4 (-Loc x Sp x Hair, -Sp x Hair)	8.185	9	−4.045	−1	0.044

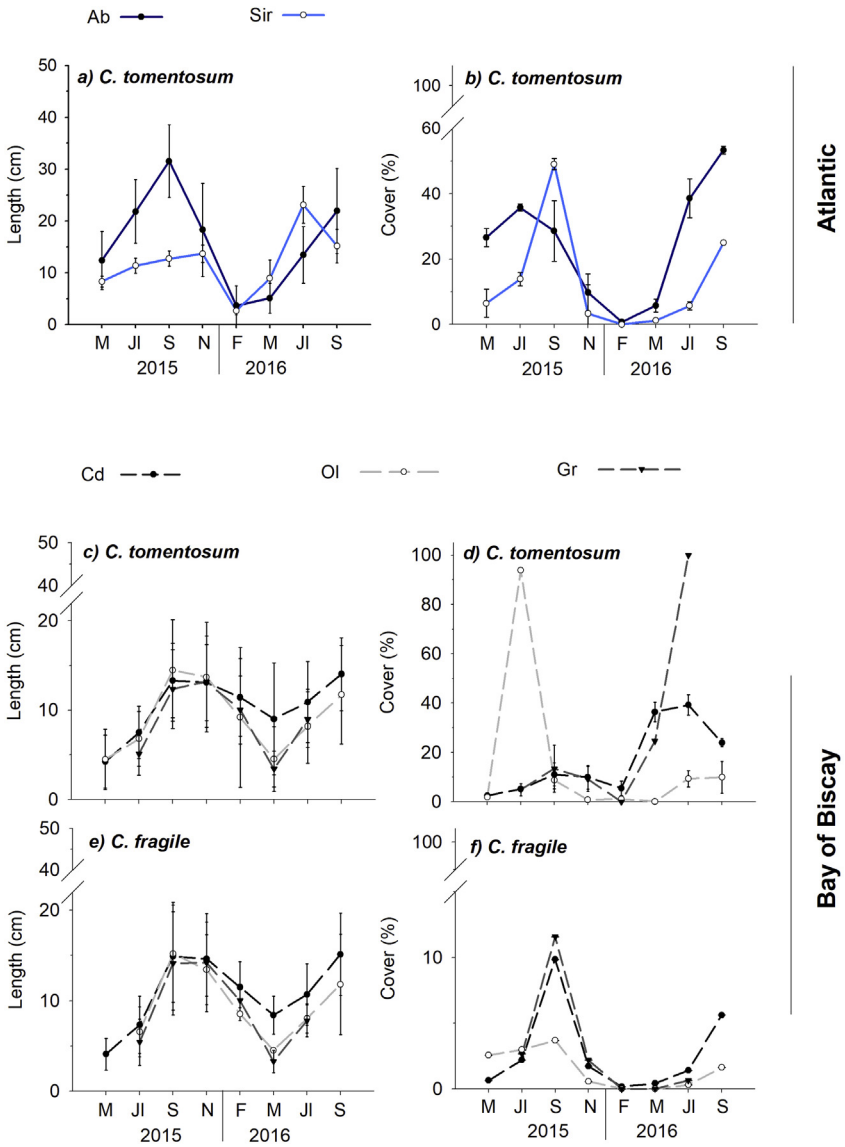

Fig. 5. Temporal patterns of thalli length and percentage cover of *C. tomentosum* and *C. fragile* in locations on western Atlantic shores (a, b) and Bay of Biscay (c–f). Abbreviations for locations as in Fig. 1. Means (± SE) values are shown. Data from different plots were pooled, n = 19–46. Note the differences in the y-axis scale for the percentage cover of *C. tomentosum* and *C. fragile* in locations in the Bay of Biscay.

and fusion respectively, n = 126).

4. Discussion

The cryptic invader *C. fragile* has long been assumed to outcompete and displace its native congeners. However, empirical evidence supporting this hypothesis is rather scarce, due to the paucity of qantitative information on the dynamics of relationships in *Codium* spp. assemblages (Trowbridge, 2001; Trowbridge and Farnham, 2009; Trowbridge et al., 2013). Our data did not support this assumption and indicated the coexistence of the invasive and native congeneric species. However, the data also indicated the potential of the exotic species to spread in a context of climate warming.

We found that on intertidal shores in most of the study locations in N-NW Spain *C. fragile* coexists with two native species, *C. tomentosum* and *C. vermilara,* as previously observed in the area (Rojo et al., 2014). Specimens of *C. vermilara* were scarce, as this species mainly occurs on the shore at shallow subtidal levels on the coasts of Spain (Ballesteros, 1989; Gorostiaga et al., 2004; Rojo et al., 2014), in contrast to the patterns observed in other regions, where *C. vermilara* was found widely distributed in the intertidal zone (Trowbridge and Farnham, 2004). Although *C. decorticatum* has previously been recorded in the study area (Gorostiaga et al., 2004), we did not find any examples of this species, which seems to be abundant in subtidal habitats (Díez et al., 2003). Furthermore, we selected semi-exposed locations on northern shores (Bay of Biscay) and western shores (Atlantic coast) (sites in the outer areas of the rias, in the latter case), to avoid confounding factors between longitudinal changes in *C. fragile* proportion and variations in wave exposure. *C. fragile* may be more abundant in inner areas of the rias, as it tends to survive and grow better in sheltered areas (Bulleri and Airoldi, 2005; D'Amours and Scheibling, 2007). Further studies focusing on *Codium* assemblages on sheltered shores and subtidal levels are needed to evaluate population trends and dynamics.

The relative abundance of *C. fragile* increased towards the Bay of Biscay, especially in July, and the increase was positively correlated with the increase in seawater temperature towards the inner areas of the Bay of Biscay. The affinity of *C. fragile* for warmer water has also been observed in other invaded regions (Trowbridge, 1996; Armitage and Sjøtun, 2017, and references therein), and a previous distribution model predicted the warmer central-eastern Cantabrian coast as the

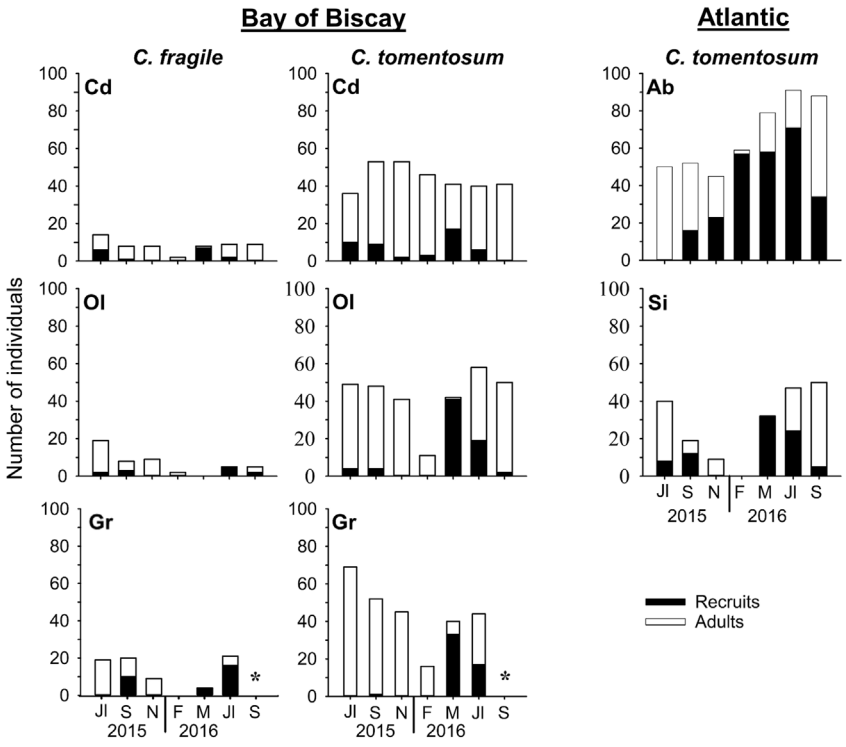

Fig. 6. Temporal patterns of the total number of individuals (and recruits) of *C. tomentosum* and *C. fragile* in the studied locations in the Bay of Biscay and western Atlantic shores (data from different plots were pooled). Abbreviations for locations are as in Fig. 1. For La Griega (Gr), the asterisk (*) indicates no data available (sampling was not conducted, because of bad weather conditions).

Table 3
Analysis of variance for the effect of Location and Year on thalli length for *C. tomentosum*. Data were balanced and log-transformed. n = 37, Loc = Location.

Source	MS	df	F	P
Loc	1.9114	4	3.3805	0.1325
Year	0.8101	1	1.4326	0.2974
Year x Loc	0.5654	4	13.8921	< 0.001
Residual	0.0407	360		

most suitable area for this species in N Spain (Tyberghein et al., 2012). Culture, filamentous forms of *C. fragile* display greater tolerance to high seawater temperature (with an optimum between 20 and 25 °C and up to 30 °C; Yang et al., 1997) and to long periods of desiccation than native congeners (Schaffelke and Deane, 2005; Kim and Garbary, 2007). This species also grows faster at higher photon levels than *C. tomentosum* and *C. vermilara* (Yang et al., 1997). The increase in SST and solar radiation experienced in the studied area in the last decades, especially during spring-summer and particularly towards the east, inner part of the Bay of Biscay (Gómez-Gesteira et al., 2008; Sanchez-Lorenzo et al., 2009; Mateos et al., 2013, 2017; Costoya et al., 2015), may be more advantageous to the invasive than to the native species. As a result of such recent environmental changes, seaweed assemblages in the Bay of Biscay are already experiencing shifts in their composition and structure, with an increase in warm-water and non-indigenous species (Díez et al., 2012). Thus, the greater tolerance of *C. fragile* to some environmental factors than that of their congeners, together with opportunistic abilities to occupy disturbance-generated gaps (Scheibling and Gagnon, 2006), may favour the establishment and spread of the exotic under a climate change scenario. In fact, *C. fragile* was cited in the Basque country in 1964; at that time, *C. tomentosum* was also apparently more abundant than the invasive species in exposed and semi-exposed locations (Van den Hoek and Donze, 1966). This dominance now appears to be reversed, with a higher proportion of the invasive *C. fragile* occurring towards inner parts of the Bay of Biscay and locations such as Kobaron with the only *C. fragile* present in the sampled plots.

The presence of *C. fragile* was clearly seasonal in the studied area, as most of the fronds die back in winter, feasibly by wave-dislodgement, while *C. tomentosum* was more persistent throughout the year. Moreover, *C. tomentosum* cover was greater than *C. fragile* cover in permanent plots in most of the study locations. However, reproduction and recruitment exhibited similar seasonal variability in the native and the exotic species. The persistence of *C. fragile* throughout the year varies among geographical regions. It is perennial in its native area (Kim, 1988; Trowbridge, 1998), whereas in the introduced area it can either be perennial or show seasonal fragmentation during winter (Dromgoole, 1975; Trowbridge, 1998; Burrows, 1991). The timing of recruitment of the two species was similar (spring-summer) to that recorded in other studies (Trowbridge, 1998; Schmidt and Scheibling, 2005), but was not consistent across locations. The exotic species presents several modes of reproduction and "recruitment", including sprouting from perennial holdfast as well as settlement of parthenogenic gametes, buds and thalli fragments (Trowbridge, 1998; Scheibling and Melady, 2008; Watanabe et al., 2009). Our data suggested that recruitment of *C. fragile* relies on new settlers rather than on vegetative regeneration from perennial holdfasts, whereas *C. tomentosum* mainly grows from perennial holdfasts. This strategy may confer a competitive advantage to *C. tomentosum* over *C. fragile* by preventing recruitment of the invasive species. The differentiation and quantification of the origins of new recruits have seldom been evaluated in *Codium* assemblages (but see Bégin and Scheibling, 2003; Schmidt and Scheibling, 2005). A higher proportion of gametangia-bearing individuals, especially of *C. fragile*, was found in February, as previously observed (Bégin and Scheibling, 2003; Schmidt and Scheibling, 2005; Rojo et al., 2014), although this pattern varied geographically and between species. Nevertheless, the importance of gametangia production and of vegetative propagation is still not clear in *Codium* species (Prince and Trowbridge, 2004), and further experimental work is necessary to elucidate the relative impotance of the different reproductive strategies.

Maximal thallus lengths were recorded in the summer period, as previously reported (Bégin and Scheibling, 2003; Schmidt and Scheibling, 2005). No differences in thallus length were detected between species, but *C. tomentosum* from locations in the western Atlantic

area had longer thalli than those from sampling locations in the Bay of Biscay. Although growth of *Codium* species seems to be driven by temperature, with higher growth rates at temperatures between 16 and 24 °C (Hanisak, 1979; Schmidt and Scheibling, 2005), other factors such as nutrient concentration and wave action may exert a strong influence (Bégin and Scheibling, 2003; Schmidt and Scheibling, 2005; Bulleri et al., 2007). In the present study, a factor that potentially explains the different sizes of *C. tomentosum* individuals is an increase in nutrient concentrations, especially nitrates and nitrites, during spring due to upwelling events that bring colder and nutrient-rich waters to the surface layers in the western Atlantic shores (Botas et al., 1990; Álvarez et al., 2010). In this context, the presence of utricle hairs, which were much more frequent in *C. fragile* in July, coinciding with the low nutrient concentrations, may confer some advantage to the invader, allowing it to grow under conditions of low nutrient availability, as *C. fragile* may be nitrogen-limited for most of the growing season (Trowbridge, 1998). Utricle hairs indeed may enhance nutrient uptake due to increments in surface area/volume ratio (Oates and Cole, 1994; Harrison and Hurd, 2001). Nevertheless, the function of these hairs is unclear and apart from enhancing nitrogen assimilation they may also provide protection against light or contribute to differences in resistance to attacks by grazers (Trowbridge, 1998).

In conclusion, the study revealed different life-cycle strategies for *Codium* species and suggests that the potential impact of *C. fragile* in the native congeners may be scale-dependent. However, so far, there is no evidence of displacement of native congeners on a large spatial scale. Although episodes of proliferation of *C. fragile* have been described in other regions in the last few decades (Bulleri et al., 2006; Scheibling and Gagnon, 2006; Drouin et al., 2011), several studies have also reported a decline in *C. fragile* abundance along European coasts (Trowbridge and Farnham, 2009; Trowbridge et al., 2013; and references therein). The increase in seawater temperature and irradiance levels already being noted, in particular towards inner areas of the Bay of Biscay (Gómez-Gesteira et al., 2008; Sanchez-Lorenzo et al., 2009; Mateos et al., 2013, 2017; Costoya et al., 2015), may favour the presence of *C. fragile* over the native congeners, with additional negative effects on native assemblages. In fact, the environmental change in this area coincide with a strong decline of cold-temperate canopy-forming species and their replacement by warm-temperate seaweeds (Díez et al., 2012; Fernández, 2016). Nevertheless, the future trends and impacts of the invasive species on native assemblages will be dependent on the long-term climate changes, and warming trends are far from being spatially and temporally homogeneous. Actually, the time period of this study coincides with a record cold surface anomaly in the N Atlantic, which peaked in summer 2015 and continued at weaker level in 2016, and increasingly strong temporal variability in ocean temperatures is suggested as a future scenario (Josey et al., 2018). Furthermore, recent projections indicate the strengthening of the coastal upwelling along western Atlantic shores (Sousa et al., 2017). Further and periodic surveys on rocky shores of N-NW Spain are essential to determine the long-term changes in *Codium* assemblages and their links to the drastic environmental and biotic alterations already taking place in the region.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.marenvres.2018.07.008.

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